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A Comparison of Beetles and Spiders Inhabiting Soil, Litter and Coarse Woody Debris in stands Originating from Harvest and Wildfire

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A Comparison of Beetles and Spiders Inhabiting Soil, Litter and Coarse Woody Debris in stands Originating from Harvest and Wildfire

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DISCLAIMER

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Abstract: Litter-dwelling and epigaeic ground-beetles (Carabidae), rove beetles (Staphylinidae) and spiders (Araneae) were sampled by pitfall trapping over two summers (1996-97) in fire- and harvest-origin sites in northeastern Alberta. More than 21,000 individual invertebrates were collected and identified to species from 12 sites representing three, post-disturbance stand ages. Two fire- and two harvest-origin stands were studied for each stand age (*i.e.*, stand initiating disturbances in 1995, 1982 and 1968).

Both stand age and origin type significantly affected abundance of rove beetles, which were most common in harvest-origin and older stands. Data for spiders and carabids showed the same trend but differences were not statistically significant. Fewer species of staphylinids were collected in the youngest fire-origin stands than from older stands, but this apparent difference in diversity is mainly a function of reduced overall sample size in these stands. Diversity of spider assemblages was higher in pyrogenic than in harvested stands that originated in 1982, but there were no significant differences in carabid diversity between stand ages or origin types. There was no overall relationship between stand-level estimates of coarse woody material and invertebrate abundance or diversity. Abundance of carabid beetles and spiders, in general, and that of several individual species could be predicted significantly from abundance of the coarse woody material, but the relationship was negative.

Both cluster analysis and ordination using Detrended Correspondence Analysis suggest that harvest- and fire-origin stands start off quite differently, with respect to invertebrate faunal composition, but converge on similar assemblages 30 years post disturbance. A general trend in the data is that harvest-origin stands actually recover more quickly toward faunal composition that resembles that in 30-year old fire-origin stands than do fire-origin stands. Thus, fire- and harvest-origin stands follow different trajectories of recovery.

More than one-third (87) of the total number of species collected (221) were unique to one stand origin type. Most of these were rare with poorly understood natural history, making interpretation of these data problematic. However, a few abundant species were restricted either fire- or harvest-origin stands. Only one, the carabid *Nebria gylenhalli*, was restricted to harvest origin stands, and this is probably an artifact of influence from an adjacent riparian site. Several species unique to fire-origin stands, including the carabids *Elaphrus lapponicus* and *Platynus mannerheimi* and the spider *Gnaphosa borea*, are damp-habitat specialists that may have survived fires in moist fire-skips. Two other carabids, found only in young

fire-origin stands, *Harpalus egregius* and *H. laticeps*, are likely early successional specialists, adapted to conditions immediately after fires.

Five recommendations are offered on the basis of this study. Recommendations for forest managers are 1) to ensure that at least some wetter microsites are left undisturbed during upland harvests and 2) to employ silvicultural practices that retain early succesional species characteristic of fire-origin stands. Research recommendations are 1) to initiate controlled experiments to compare directly harvest and wildfire effects on invertebrate assemblages, 2) to develop the biological knowledge required to use invertebrates as indicators of recovery after harvest, and 3) to initiate focused work on the relationships between coarse woody material and the diversity and abundance of forest invertebrates.

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Introduction

Background and Literature Review

Invertebrates inhabiting soil, litter, and coarse woody debris are vital elements of forest ecosystems. They play crucial and well-documented roles in decomposition of coarse and fine organic matter, nutrient cycling, maintenance of soil structure and regulation of potential forest pests (Price 1973; Szyszko 1974; Petersen & Luxton 1982; Spence 1985; Speight 1989; Stork 1990), and thus are thought to influence long-term forest productivity and sustainability. Invertebrates are also important as a food resource for highly valued forest vertebrates (summarized by Wilson 1992). Recently, for example, Pettersson et al. (1995) have shown that regenerated plantations in Sweden provide far fewer of the invertebrates essential for passerine bird assemblages than do naturally regenerated forests of the same age. They attribute well-documented reductions in Scandinavian forest passerines to stand-level changes in invertebrate production brought about by several harvest rotations. Thus, the extent to which forest invertebrate communities are affected by forestry practices has serious ecological implications, and is of concern to forest managers.

Forest disturbances such as harvesting and fire alter various physical, chemical, and biological factors in the litter and soil (Sims 1976; Kubin & Kemppainen 1991; Cortina & Vallejo 1994) and coarse woody debris (Muona & Rutanen 1994). These alterations, in turn, modify habitats for the invertebrates living there. A number of studies in other forest ecosystems have shown dramatic effects of logging and fire on invertebrate communities inhabiting soil, litter, and coarse woody debris (e.g., Huhta 1971; Vlug & Borden 1973; Lenski 1982; Heliovaara & Vaisanen 1984; Speight 1989; McIver et al. 1992; Niemela et al. 1993a, b; Langor et al. 1994; Siitonen & Martikainen 1994). In Alberta, economic development of the boreal mixedwood is subject to major economic development (Peterson & Peterson 1992; Stelfox 1995), and in the north, large tracts of virgin forest are now allocated to FMAs and slated for harvest. These developments have generated legitimate concerns about the ecological resilience and sustainability of these forests in the wake of extensive harvesting.

There is currently a widespread movement to embrace a "natural disturbance model" for harvest of forests on an "extensive land base" that are not managed intensively for maximum fibre production, as reflected by the Alberta Forest Conservation Strategy. Proponents argue that use of harvest regimes resembling the spatial pattern of disturbances on forested landscapes will ensure conservation of biodiversity while permitting extraction of economically desirable volumes of fiber (Hunter 1993; Bunnell 1995). In Alberta, these disturbances are to be modeled mainly as wildfire, as these are the most obvious and most easily re-constructed of several possibly important disturbances. Others, however, point out that fire and harvest are not ecologically equivalent, especially with respect to effects on invertebrate faunas (Zackrisson 1977, Muonaa & Rutanen 1994, Spence et al. 1996, 1998). Thus, biotic components critical to ecosystem function may be at risk in landscapes harvested without consideration of ecological processes in detail, no matter what *pattern* of cutting is adapted. Despite the logical appeal of the natural disturbance model, it has not been well tested (Alpert 1995), clearly embodies several oversimplifications (Haila 1994) and the fire-based model fails to incorporate effects of forest renewing processes in addition to fire (e.g., Holling 1992). Hence, there is a need to determine whether succession from burned and logged sites generates forest structure suitable as habitat for the normal mixedwood biota. If, for example, stand-level processes like those documented by Pettersson et al. (1995) lead to reductions in abundance of food for larger wildlife, their populations sizes will surely decrease, no matter what harvest pattern is imposed on the landscape.

Wilson (1992) argues that resilience of ecosystems depends on biodiversity. Thus, it is proper that we endeavour to understand how forestry activities affect the diversity as well as the distribution and abundance of species that comprise forest communities. Invertebrates comprise 80-85% of the world's described species and this fact alone argues that we should give them serious attention in forest ecosystems. In order to best conserve biodiversity in our forests, we must first understand it, and then develop the knowledge essential to integrate land management and forestry practices in a way that conserves it (Brussard 1991; Probst & Crow 1991). To contribute towards this knowledge base, and to specifically test the natural disturbance model, we have investigated the relative effects of harvesting and fire on beetle (Coleoptera) and spider (Araneae) assemblages associated with soil, litter, and coarse woody debris in aspen-dominated mixedwood forests in north-central Alberta.

Beetles are ideal organisms for understanding the effects of disturbances on forest ecosystems. They are among the most conspicuous and abundant groups of arthropods in boreal communities (Danks & Footit, 1989) and assemblages inhabiting litter and coarse woody debris (Fager 1968; Hammond 1996; Spence et al. 1996) are relatively easy to sample and identify in relation to other arthropods. Beetles fill many trophic roles including predators, fungivores, herbivores, scavengers, and woodborers (Hammond 1996), and are increasingly linked to population performance of valued forest vertebrates (Martikainen et al. 1997). They also are highly sensitive to habitat changes (e.g., Thiele 1977; Niemelä 1990; As 1993, Hammond 1996), especially those resulting from forest cutting (Lenski 1982; Szyszko 1983; Heliovaara and Vaisanen 1984; Niemelä et al. 1988, 1993a, b; Hammond 1996, Spence et al. 1996). Because of their sensitivity to environmental variation, beetles and spiders are potentially good 'indicator' species for assessing the effects of habitat perturbations (Eyre et al. 1989; Eyre & Rushton 1989). Some beetles and all spiders are also predators of forest pests (reviewed by Thiele 1977) and, along with other epigaeic arthropods, influence the structure of soil and litter communities responsible for soil structure, nutrient cycling, and site fertility (Szyszko 1974; Spence 1985, Speight 1989; Stork 1990). In short, these two litter-dwelling taxa are taxonomically diverse groups with strong links to forest function. Thus, detailed study of their assemblages may provide an effective model of arthropod response to forestry practices, especially in relation to the critical issue of residual material that is left on site.

To test the generality of the beetle model, we propose addtional work with spiders, another diverse group receiving growing attention in relation to forestry impacts (e.g., Huhta 1971; Jennings & Collins 1987; Mason 1992; McIver et al. 1992; Pettersson 1996). Spiders also offer excellent potential as biodiversity indicators as they are unbiquitous, easily sampled and fill a key, upper-level trophic niche linked availability of phytophagous prey and overall community productivity (Clarke & Grant 1968; Van Hook 1971, Wise 1979). Furthermore, as is the case for several families of ground-dwelling beetles, spider species range in abundance from rare specialists to abundant and common forest generalists. Litter-dwelling spiders are sensitive to litter depth and habitat complexity (Utez 1991), a feature significant to this comparison of harvest- and fire-origin stands because these processes both alter litter and soil development, but may do so in different ways.

Objectives

The research reported here has been executed in the context of a larger multi-disciplinary, multi-agency project titled "The effect of wildfire and timber harvest residuals on biodiversity, and forest stand/landscape structure in aspen-mixedwood communities in Alberta" commenced in 1995 under the leadership of P. Lee at the Alberta Environmental Centre. As a contribution to this larger study, we have 1) compared the abundance, diversity and structure of spider and beetle assemblages among fire- and harvest-origin aspen-mixedwood stands; 2) studied how assemblages change over time since disturbance and sought to identify faunal components that may be particularly sensitive to differences between burning and harvest; and 3) tested the hypothesis that spatial variability in arthropod assemblages is influenced by the amount of stand residual left in the wake of harvest or wildfire. Work toward these three objectives is integrated by comparing trajectories of community recovery in response to both disturbance types among three age classes of regenerating stands.

Methods

Study Area

We studied 12 stands located in the boreal mixedwood region of Alberta (Fig. 1). The forests in this region are dominated by trembling aspen (*Populus tremuloides* Michx.). Other overstorey trees include balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* [Moench] Voss), and birch (*Betula* sp.). Six of the stands regenerated naturally after wildfire and six regenerated without intensive silvicultural intervention after harvest. Collectively, three age classes were represented: stand origin in 1995, 1982, and 1968. The resulting design therefore has two treatment types (origin type and age class) with two stands sampled for each treatment combination. These age-classes are representative of the early succession of mixedwood forests in Alberta. Site codes, descriptions, and locations are given in Table 1.

The design of the study is largely constrained by the existing number, size, age, and relative proximity of harvested and pyrogenic aspen-mixedwood stands. The oldest suitable harvested stands available are 20-30 years old, thus limiting age class comparisons to this age or younger. Stands were chosen by P. Lee and associates (Alberta Research Council, Vegreville) using forest inventories, aerial photography and ground truthing (Lee 1997). These sites are spread out over a wide geographical area in northeastern Alberta, and thus interpretations of resulting data may be confounded by geographical variation. However, this is the best that can be done with a chronosequence study of aspen forest, given that harvest of aspen was rare in Alberta before the late 1980s. The original tree composition of disturbed stands was ascertained by assessment of tree composition of adjacent undisturbed stands, and stands selected for comparing disturbance effects within age classes were selected to be as similar as possible. All 12 stands are presently dominated (*i.e.*, >80% of stems) by aspen but appear to have originated from stands with a greater component of spruce.

Sampling

Litter and ground-dwelling taxa of three taxonomic groups, ground-beetles (Carabidae), rove beetles (Staphylinidae) and spiders (Araneae), were sampled using continuous pitfall trapping in 1996 (year 1) and 1997 (year 2). The length of the trapping period varied between years and sites. Sampling occured from June 3 to September 24 in year 1, and from May 5 to September 23 in year 2. Average number of trapping days per trap was 90 in year 1 and 113 in year 2. One trap-line, consisting of six pitfall traps, was placed in each stand. Traps were white plastic containers 10 cm in diameter, containing 2-3 cm of ethylene glycol (see Spence and Niemela 1994 for details). Traps were place *ca.* 50 m apart to ensure independent samples (Digweed et al. 1995). A plywood "roof" measuring 15 x 15 cm was suspended on corner nails 2-3 cm above the traps to prevent flooding, accumulation of excess leaf material, and to protect against disturbance. Traps were serviced at 10-15 day intervals throughout the collection period and thus samples are similarly aggregated.

In summer 1997 a vegetation survey was completed at each pitfall trap location. Percent cover of plant species were estimated in a 5 x 5 m plot around the pitfall trap. Percent shade, litter depth and biomass were also estimated using protocols outlined by Niemelä and Spence (1994). The potential value of these data for predicting distribution and abundance of epigaeic invertebrates will be analysed in the near future and included in subsequent publications but these analyses are unavailable at the time of this report.

Analyses

Data about abundance were pooled for the two years and adjusted to represent the catch from 500 trap days in each stand. Differences in abundance of each taxon were then tested using a 2-factor ANOVA with stand origin (fire or harvest) and stand age (originating in 1995, 1982, or 1968) as main effects. Data from each trap-line were pooled for tests of abundance.

To compare species richness among stands the data was adjusted to compensate for varying samples size. These adjustments were made by rarefaction which is a statistical method for estimated the expected number of species in a random subsample drawn from a larger sample (Simberloff 1978). The resulting value can be interpreted as a diversity index as both species richness and relative abundance are taken into account.

Data from standardized catches were used for cluster analyses to group stand types based on the similarity of the spider community. Pair-wise similarities are based on the Bray-Curtis Index for percent similarity and clusters were formed using unweighted arithmetic averaging.

Pitfall trap data was further analysed using detrended correspondence analysis (DCA). This ordination technique is useful is assessing patterns in community strucure. Individual pitfall traps were used a sample points. Since some pitfall traps were frequently disturbed throughout the collection period, only traps with greater than 75 trapping days were used in the analysis.

We tested for possible effects of volume of coarse woody debris (CWD) on species richness and abundance of various taxonomic groups using standard linear regression. For these analyses, we regressed the median estimate of either species richness or abundance from trap-wise data for each stand on estimates of CWD volume for each stand as provided by the interim report for the Fire and Harvest Residual Study (Lee 1997).

Results

A rich data base resulted from fieldwork conducted during the summers of 1996 and 1997. More than 21,400 individual arthropods representing 221 species have been identified. This includes 6,194 ground-beetles representing 38 species, 7,840 rove beetles representing 76 species and 7,387 spiders representing 107 species. These taxa are among the most numerous and diverse elements the macroarthropod fauna of leaf litter habitats in northern forests. Therefore, analysis of this data base provides an excellent opportunity to answer the questions suggested by the objectives of our original research proposal to the Manning Diversified Research Trust Fund. The following presentation is structured in terms of these three objectives.

Abundance, Diversity and Structure of Assemblages

Abundance. Analyses of variance revealed statistically significant effects of both stand age (F=12.3, df=2, 6, p<0.01) and origin type (F=11.1, df=1, 6, p<0.02) on abundance of rove beetles. The analysis indicates no significant interaction effect (F=0.60, df=2, 6, p=0.58) so clearly the effect of origin type does not depend on stand age. Overall, staphylinids were more abundant in harvest-origin stands and in stands of the two older age classes (Figs. 2 and 3). This trend is also seen in data for both ground-beetles and spiders, but mean differences are smaller and not statistically significant. Clearly, rove beetles were much less abundant in the youngest stands and reached their maximum abundance in the oldest stands (Fig. 3). For spiders, on the other hand, mean abundance was highest in the youngest stands, although spider abundance did not vary significantly over stand age. Mean abundance of carabids showed the interesting pattern of lowest abundance in the intermediate aged stands.

Diversity. Rarefaction estimates of species diversity show that overall diversity of litter dwelling arthropods did not differ dramatically between fire and harvest origin stands at any age (Figs. 4-6). Certainly the estimates of species number for each group were statistically indistinguishable between the oldest fire- and harvest-origin stands. Number of rove beetle species was conspicuously lower in the youngest fire-origin stands than for comparably aged harvest origin stands (Fig. 4b), but this is mainly a function of their significantly lower abundance. If the rarefactions are carried out for all stands using a base of 200 individuals, which is far below the captures observed in older stands, the species diversity of the youngest stands does not appear to be affected by stand origin type (Fig. 4a). The diversity of spider assemblages was significantly higher in fire-origin than harvest-origin stands that originated in 1982 (Fig. 6). The expected number of carabid species did not vary significantly with stand origin for any stand age class (Fig. 5).

Assemblage structure. We use cluster analysis of the straight-forward and widely used Bray-Curtis index based on the relative abundance of species to illustrate the overall pattern of similarity for these invertebrate assemblages with respect to stand age and origin combinations. Overall, the results suggest that pyrogenic and harvested stands tend to converge on similar species associations over time as the highest similarity values generally occur among the oldest stands. In the analysis of all taxa (Fig. 7), the two treatments originating in 1995 were only 37.2 % similar to the combined sample from older treatments and clustered together only at 51.2 % similarity. This underscores that the litter-dwelling invertebrate fauna is profoundly affected by disturbance and that traditional harvests and wildfire affect the faunal in rather different ways. The cluster topology is somewhat more difficult to interpret for the 4 older stand age-origin combinations. However, the highest similarity (72.4 %) was between the 1968-Fire and 1982-Harvest samples, but the 1968-Harvest samples clustered at 66.5 % similarity. The 1982-Fire samples, on the other hand, are only 47.2 % similar to the three-component cluster of the other older stands. This topology suggests that pyrogenic stands lag behind harvest-origin stands in faunal recovery.

The patterns differ somewhat among the three-taxon data set and the separate taxon-specific analyses (Fig. 8 a-c). As in the overall analysis, the three separate analyses consistently show that most recently disturbed stands are remarkably dissimilar to that older stands, again suggesting that invertebrate faunas do converge with time. Staphylinids (Fig. 8b) are most affected immediately (similarity of 1995-Fire and 1995-Harvest is 44.0 %) by disturbance type, whereas carabids (Fig. 8a) are the least affected showing a similarity value of 58.8 % between the 1995 fire- and harvest-origin stands. Rove beetle and spider assemblages reach relatively high maximum similarity values (77-79 %) but the maximum similarity attained by carabid assemblages was 66.1 %. Thus, over the long run staphylinid and spider assemblages may be less sensitive to disturbance type (*i.e.*, fire vs. harvest) but serve as good overall monitors of stand recovery. Carabid assemblages, on the other hand, seem to be somewhat less immediately affected by disturbance per se, but show long-lingering effects of disturbance type.

Faunal Changes and Sensitive Components.

We've used detrended correspondence analysis (DCA) (ter Braak 1987a,b) to further describe the trajectory of change in these assemblages. The overall analysis (Fig. 9) depicts individual trap data about all three taxa in ordination space defined by the first two DCA axes. The first axis, which has a relatively high eigenvalue, separates the stands more-or-less with respect to age. The convergence of faunal assemblages from the 1968-Fire and the two oldest harvest-origin sites is apparent on the right side of the diagram, although some trap-sites from the 1968-Harvest sites depart from the main grouping by being distributed upward along the second DCA axis. As would be expected from the results of the cluster analysis, the 1982-Harvest and 1968-Harvest stands are closer together in the ordination than are the comparable fire-origin stands. Their separation is mainly along DCA axis 2. The 1982-Fire and 1995-Harvest sites are less separated along DCA axis 1 than along axis 2. Axis 2 then seems to reflect sensitivity to disturbance type that develops *after* disturbance. Note that 1995-Fire and 1995-Harvest sites show little separation along axis 2. Fire- and harvest-origin assemblages start off from overlapping points in this ordination-space, they appear to follow diverging trajectories before finally converging in the oldest stands. Thus, both cluster analysis and ordination support the claim that litter invertebrates converge with respect to general community structure by 28 years post-disturbance. However, given that the two chronosequences followed quite different trajectories to reach the present positions in ordination space, it is risky to predict that community development will be parallel in fire- and harvest-origin stands in the future.

The taxon specific axes (Figs. 10a-c) are generally similar to the overall ordination. Unlike the cluster analysis, which suggested lingering sensitivity to disturbance type in carabids, the DCA plot (Fig. 10a) shows reasonably similar, albeit widely spaced, patterns for similar-aged communities, regardless of disturbance type. Staphylinid assemblages appear to converge in 30-year old stands of fire and harvest origin but the DCA plots suggest that they follow different pathways in getting there with 1982-Harvest stands closer to the 30-year points than those from 1982-Fire stands (Fig. 10b). A similar pattern is apparent for spiders (Fig. 10c). Especially for spiders and staphylinids, the broad dispersion of points from the 1995 stands suggests that response to disturbance could depend rather dramatically upon microsite characteristics, *i.e.*, note higher levels of variation in the 1995-origin stands as compared to older stands.

From a biodiversity perspective, however, we must ultimately get down to the level of species in a search for taxa that may be particularly sensitive to disturbance types. Some species of each taxon are collected only in stands of one age or origin type (Table 2). In summary, 87 species were unique to one stand origin type. Overall, 36 species (8 carabids, 9 staphylinids and 19 spiders), or c. 41% of the unique species, were found only in fire-origin stands, and 51 species (9 carabids, 15 staphylinids and 27 spiders) were collected only from harvest origin stands. Most (81) of these are records of 1-5 individuals and must be presently discounted because biological understanding is insufficient to interpret the meaning of their presence. These may be rare species with unique habitat requirements, but alternatively could be stragglers captured at particular sites mainly through chance. Further work is required to interpret such information and these species will not be further discussed here.

Six species (5 carabids and 1 spider; see Table 2), however, were more abundant in stands of a single origin type. The carabid, *Nebria gyllenhali*, was found only in 1968-Harvest stands. Four carabids, *Elaphrus lapponicus*, *Harpalus egregius*, *H. laticeps* and *Platynus mannerheimi*, were collected only from fire origin stands. All but *P. mannerheimi* were found in the youngest pyrogenic stands; the two *Harpalus* species were restricted to these but *E. lapponicus* was also taken in the 1982-Fire stands. P. mannerheimi, on the other hand, was found only in the oldest fire-origin stands. The spider, *Gnaphosa borea*, was restricted to pyrogenic stands but was found in all three age classes of this stand origin type.

Spatial variability of the fauna and habitat characteristics.

Species richness of all three taxa combined (r=-0.29, n=12, p=0.36) or of Staphylinidae (r=-0.12, n=12, p=0.71) was not significantly affected by volume of CWD. However, species richness of both Carabidae (r=-0.60, n=12, p=0.04) and Araneae (r=-0.54, n=12, p=0.07) seemed to vary inversely with the gross, stand-wise estimates of CWD volume available (Fig. 11).

There were no significant (r= -0.32 to 0.03, n=12, p=0.31 to 0.94) relationships between volume of CWD and abundance of all three taxa combined or any of the individual higher taxa. Among commonly collected species, abundance of only the staphylinid, *Oxytelus fuscipennis,* was significantly related to volume of CWD (r=-0.59, n=12, p=0.04) and it showed a pronounced decrease as volume of CWD increased in the various stands (Fig. 12). With only stand-wise comparisons possible, given the existing CWD estimates, the data are relatively weak for this purpose. Nonetheless, negative regression coefficients were more common for abundant species than were positive coefficients.

Discussion/Conclusion

Recently burned and recently harvested stands are quite dissimilar to most observers. The question for those interested in managing forests in the context of the new emerging sustainability criteria is whether such differences throw biotic succession onto different courses that might threaten some of the biota. As part of a team of forest ecologists, we set out to determine how close succession from burns and harvests might be in the aspen-dominated mixed wood. We asked whether harvest was a reasonable substitute for fire with respect to development of the litter-dwelling invertebrate fauna. If so, we reasoned that fire- and harvest-origin stands would develop increasingly similar faunas as they aged. If the fauna diverged significantly, however, the logic of using harvest as an analogue for fire may be flawed with respect to protection of biodiversity.

Data from this study support the general thesis that epigaeic arthropod assemblages in harvest-origin stands become increasingly similar to those of fire-origin stands with time. Clearly, the abundance and species composition epigaeic fauna of aspen-dominated mixed wood stands becomes increasingly similar between harvest- and fire-origin stands over a 30 year period after stand initiating disturbance. However, conclusions about how closely former harvests have resembled wildfires as stand initiation processes depends on how the results about faunal development are weighed.

The detailed trajectories of faunal recovery varied among the three taxa studied, suggesting that they provide different information about faunal responses to disturbance. Rove beetle assemblages were markedly reduced and significantly changed from their former structure immediately after wildfire, but even the 1982-Harvest stands had developed staphylinid assemblages that were reasonably similar (c. 70%) to the oldest stands. Although spider numbers fell dramatically in the first post-fire year they had largely recovered by the second season and remained relatively high in the fire-origin stands. The structure of spider assemblages of the 1995-origin stands differed conspicuously between the two origin-types (c. 50% similarity), although they were more similar to each other than to the other stands (c. 38% similarity). As with staphylinids, spider assemblages of the 1982-Harvest stands converged toward the structure seen in the oldest stands at about 70% similarity. Carabid assemblages seem to show the least immediate response to disturbance type, probably reflecting the influence of residual populations. Nonetheless, these residual populations slowly disappear, and among the three taxa treated in this report, ground-beetle assemblages seem to show the most marked response to differences between harvest and wildfire 30 years after disturbance.

Six reasonably common species were identified as strongly associated with either burned or harvested stands and data about them provide the strongest contrasts between harvest and wildfire as stand initiating processes. Furthermore, because biological information is available for some of these species, there is basis for conjecture about the meaning of the data.

Of the six common species unique to one origin type, only a single carabid species, *Nebria gyllenhali*, was abundant and unique to harvest origin stands. All specimens were taken from a single 1968-Harvest stand suggesting possible influence of a local site effect. *N. gyllenhali*, as is the case for many *Nebria* species (Spence 1979), is usually found in riparian situations. However, the *Nebria* may use pupation sites far removed from water (Spence, personal observation) and high water can force adults to temporarily abandon riparian area for upland areas. These observations suggest that it is unlikely that *N. gyllenhali* is particularly favoured by forest regeneration after harvest. On the other hand, recent work in our laboratory by M.Sc. student K. Gandhi suggests that another *Nebria* species, *N. carassicornis*, survives sub-alpine wildfires in large fire-skips associated with wetter areas. It appears that individuals of *N. crassicornis* move out into older regenerating forests although their populations remain centred on the wetter areas. The presence of *N. gyllenhali* in the samples 1968-Harvest sites, at any rate, probably reflects the proximity of the traps to wet or riparian areas.

The five remaining species that were both commonly collected and unique to a stand-origin type were found only in fire-origin stands. These include two *Harpalus* species, *H. egregius* and *H. laticeps*, characteristic of early successional communities. These species may depend on fire to generate suitable habitats. The other two carabids, *Elaphrus lapponica* and *Platynus mannerheimi*, are both strongly associated to with wetter forest patches although neither is strictly riparian. Such species might persist in natural fire-skips and then be available to colonize other areas as the canopy closes in a regenerating stand. The spider *Gnaphosa borea* was found only in fire-origin but over the full range of stand ages. Published information about the biology of *G. borea* is limited but it is known mainly from wetter sites (Platnick & Dondale 1992; Koponen 1994) in eastern Canada, and thus might share membership in fire-skip communities along with the two carabids mentioned above. These species might then be excellent indicators of the suite of conditions associated with stand initiation by wildfire. The persistence of such species could be threatened on landscapes dominated by harvesting, especially if fire suppression is effective enough to prevent large, contiguous areas of mixed wood forest from burning over long intervals. Silvicultural practices on harvest-origin stands that kept these species in the system would improve the emulation of natural processes with respect to faunal development.

The results about relationships between CWD and development of the epigaeic fauna are puzzling and unexpected. In short, this work demonstrates little compelling association between the amount of CWD in a stand, after either fire or harvest, and several measures of epigaeic faunal abundance or diversity. When significant associations were found, they were generally negative. This is in clear contrast to the emerging picture for saproxylic insects (Siitonen & Martikainen 1994, Spence *et al.* 1997). Although saproxylic beetles were also collected as part of the present study, resources available for this work were insufficient to sort, process and identify the material for inclusion in this report. Therefore, discussion of associations between invertebrate assemblages and CWD in this report must be restricted to epigaeic invertebrates, most of which do not depend directly on CWD during their life-cycles.

Before accepting the unlikely hypothesis that amount of CWD in a stand has no effect on the abundance or diversity of epigaeic species or actually influences these measures negatively, a at least two alternative hypotheses that could also explain the data presented here must be rejected. Firstly, it is possible that extensive amounts of CWD on the ground, as was characteristic of the older fire-origin sites, could act as barriers that reduce the catch of pitfall traps. The assumption that activity, as measured by pitfall traps, is proportional to abundance underlies the sorts of arguments presented above (Spence & Niemelä 1994). This assumption may be incorrect at the high end of CWD abundance. Secondly, the CWD data analysed here may be matched at the wrong scale to detect real effects. The data about CWD is for the entire stand, but the replicated data about invertebrate assemblages were collected from individual pitfall traps. Unfortunately, unambiguous data about CWD specific are unavailable for each trap site and so we analysed the invertebrate data as medians of six traps for each stand. Thus, much potential information is not included in the present analysis.

Recommendations

Forest Management

The following two recommendations spring from the work reported here and would seem to be appropriate for immediate consideration by forest managers.

1. *Adjust harvesting practices in upland areas to ensure that a range of sizes representing wetter microsites are left undisturbed.* — In a number of northern forest types throughout the world it is being recognized that isolated wet forest patches, often skipped by wildfires, provide important storehouses for biodiversity (Anglestam 1997). Not only are these centers for species with habitat preferences for we areas, but these sites may also retain deep-forest specialists in cutovers, facilitating rapid recolonization with canopy closure. Data presented above, suggest

that these features characterize the epigaeic fauna of the aspen-dominated mixed wood, and that negative faunal effects can be reduced by ensuring that a suitable range of wet patches are left in the wake of logging.

2. *Employ, at least on some sites, silviculture practices designed to retain early successional species characteristic of fire-origin stands.* — Our data suggest that there are species that specialize in early successional habitats left in the wake of wildfire, and that some such species will fail to establish and colonize harvested sites that are unburned. Furthermore, the abundance of CWD left on harvested sites seems to retain more of the deep forest fauna and short-cut development of faunal assemblages as have been generally associated with recovery from wildfire. If large contiguous landscapes of the mixed wood are protected from wildfire for significant temporal intervals, these species could be extirpated from broad areas and be then unavailable to colonize stands subsequently burned within those landscapes. Some carefully regulated burning on cutovers may be required to ensure the persistence of these species and the potentially important ecological processes with which they may be associated.

Research

The research undertaken in this project has revealed deficiencies in understanding that can be resolved only through further work. Clarification of such issues holds promise for additional improvement of forest management in Alberta, and thus we recommend that research dealing with the following three specific matters be given high priority.

1. *Immediate effects of harvest and wildfire on invertebrate assemblages should be studied directly through controlled field experiments.* — Such work is necessary to ensure that interpretations of our data are not confounded by spatial and temporal variation. Furthermore, in experimental work undertaken in the present context modern harvesting techniques can be carefully and consistently applied to evaluate what we are actually doing today, rather than measure post-hoc the effects of a range of things done yesterday. Most importantly perhaps, experimental studies can be directly linked to work about ecological processes done on the same sites. Only in this way, is it possible to anticipate if important aspects of ecological function may be negatively impacted in the medium to long term by a managing for sustainability

through emulation of natural processes. Fortunately, two operational scale field experiments aimed directly at these issues are now underway in northern Alberta. Support for such experiments is further justified by the present research.

2. *Research should be undertaken to develop the biological knowledge required to use epigaeic invertebrates as indicators that could be used to monitor forest recovery after harvest.* — Five relatively common species identified in this research are associated with fire-origin stands but are apparently missing from stands regenerated after harvesting. Specific investigations of the population biology and ecological roles of these species are required to support their possible use as indicators of forest health commensurate with sustainability. In addition, a further 81 rare or uncommon species were found associated with only fire- or harvest-origin stands. Biological information about these species is required to understand if they are important considerations in forest management. Such research would also contribute to development of sampling and analytical procedures urgently required to ensure that rarely collected but ecologically important species are not overlooked in development of management protocols aimed at sustainability. Such work is a critical step in using conservation of biodiversity as a proxy for detailed functional understanding of forest ecosystems.

3. *Work to establish predictive relationships between coarse woody material (CWD) and the diversity and abundance of forest invertebrates should be undertaken in Alberta.* — Data of the sort alluded to above (Discussion/Conclusions) are required to understand likely connections between epigaeic invertebrates and local variation in abundance and quality of CWD. Information about saproxylic insects should be also developed and analysed together with data about epigaeic species. In the midterm, we should aim to connect such understanding to work about site productivity, soil fertility and nutrient cycling because these are widely recognized as an important functional manifestations of these components of forest biodiversity.

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Table 1. Study sites: description, codes, and locations

Stand type	Year of stand origin	Stand No.*	Stand code	Approximate location	Latitude and longitude
Wildfire	1995	1	F95-1	Southwest of Ft. McMurray	N56°17 W111°46
Wildfire	1995	3	F95-3	North of Mariana Lake	N56°07 W111°57
Wildfire	1982	2	F82-2	West of Red Earth Creek	N56°31 W115°52
Wildfire	1982	3	F82-3	Southwest of Ft. McMurray	N56°19 W111°51
Wildfire	1968	1	F68-1	South of Mitsue Lake	N55°11 W114°47
Wildfire	1968	3	F68-3	South of Calling Lake	N55°08 W113°20
Harvest	1995	2	H95-2	North of Calling Lake	N55°21 W113°31
Harvest	1995	3	H95-3	North of Lawrence Lake	N55°03 W113°39
Harvest	1982	2	H82-2	North of Slave Lake	N55°33 W114°48
Harvest	1982	3	H82-3	Northeast of Slave Lake	N55°26 W114°40
Harvest	1968	2	H68-2	Northeast of Slave Lake	N55°26 W114°41
Harvest	1968	3	H68-3	South of Slave Lake	N55°12 W114°41

*replicate number based on initial set-up of the Fire and Harvest Residual Study (two out of three potential replicates used for this study)

Table 2. Species found only in stands of either fire or harvest origin.

A. Species found only in fire-origin stands

Species	No. Specimens	1995	1982	1968
CARABIDAE				
Amara errata	1	X		
Amara familiaris	1	X		
Elaphrus lapponicus	7	X	X	
Harpalus egregius	25	X		
Hapalus laticeps	9	X		
Platynus mannerheimi	26			X
STAPHYLINIDAE				
Mycetophorus nigrans	2		X	
Miscodera arctica	2	X	X	
Paederus littorarius	1		X	
Philontus politus	1	X		
Pcynoglypta aptera	1			X
Quedius brunnipennis	5		X	X
Quedius frigidus	3	X	X	
Tachinus vergatus	1			X
Tachyporus flavipennis	1	X		
ARANEAE				
Arctosa emertoni	3	X		X
Ceratinella alaskae	1			X
Ceratinella brunnea	2	X	X	
Clubiona furcata	1	X		
Clubiona moesta	1		X	
Gnaphosa borea	29	X	X	X
Haplodrassus signifer	2	X	X	
Hyposinga rubens	3	X	X	
Larinioides patagiatus	1		X	
Micaria tripunctata	1		X	
Orodrassus canadensis	1		X	
Pityohyphantes costatus	2	X	X	
Thantus formicinus	1	X		
Tibellus oblongus	1		X	
Walckenaeria atrotibialis	1			X
Walckenaeria exigua	1		X	
Walckenaeria karpinski	1			X
Xysticus durus	2	X		
Erigoninae sp. D	1	X		

Table 2, cont'd.

B. Species found only in harvest-origin stands

Species	No. Specimens	1995	1982	1968
CARABIDAE				
Amara lunicollis	3	X		
Badister obtusus	1	X		
Bembidion nigripes	1	X		
Calathus advena	5	X	X	X
Cymindis cribricollis	5	X	X	X
Harpalus somnulentus	1			X
Nebria gyllenhali	83			X
Synuchus impunctatus	3	X		X
Trichocellus cognatus	1	X		
STAPHYLINIDAE				
Bolitobius sp. B	4	X	X	
Carphacis nepigonensis	1	X		
Erichsonius nanus	1		X	
Eucnecosum tenue	3	X		
Lordithon bimaculatus	1	X		
Megarthrus angulicollis	1		X	
Micropeplus laticollis	1		X	
Olophrum boreale	2	X		
Omalium sp. B	1	X		
Philontus concinnus	1	X		
Philontus cruentatus	1	X		
Quedius criddlei	3			X
Quedius nevadensis	1	X		
Tachyporus abdominalis	2			X
Tachyporus nitidulus	1	X		
ARANEAE				
Clubiona openogo	2		X	
Clubiona sp. A	1			X
Cnephalocotes obscurus	1	X		
Collinsia clypiella	1		X	
Drassodes neglectus	1	X		
Drassyllus niger	1			X
Ero canionis	1		X	
Evarchi hoyi	1	X		
Gonatium crassipalpum	4	X	X	X
Hahnia arizonica	1		X	
Neriene clathrata	3		X	X

Table 2, cont'd.

B, cont'd. Species found only in harvest-origin stands

Species	No. Specimens	1995	1982	1968
ARANEAE, cont'd				
Oreonetides rectangulatus	1	X		
Pardosa furcifer	1	X		
Pardosa tesquorum	4	X		
Pardosa sp. A	2	X		
Pocadicnemis americana	1			X
Scironis tarsalis	2			X
Sisicotus nesides	1			X
Thantus striatus	3	X		
Theridion sexpunctatum	2		X	X
Xysticus britcheri	1	X		
Xysticus canadensis	1			X
Xysticus ellipticus	1	X		
Xysticus ferox	1	X		
Erigoninae sp. A	1	X		
Erigoninae sp. B	1			X
Erigoninae sp. C	1		X	

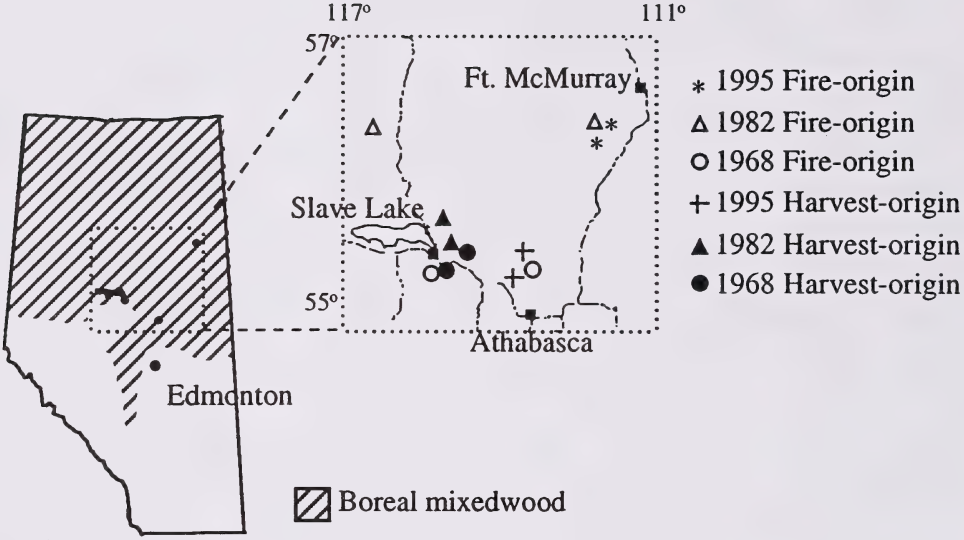


Figure 1. Approximate location of study sites

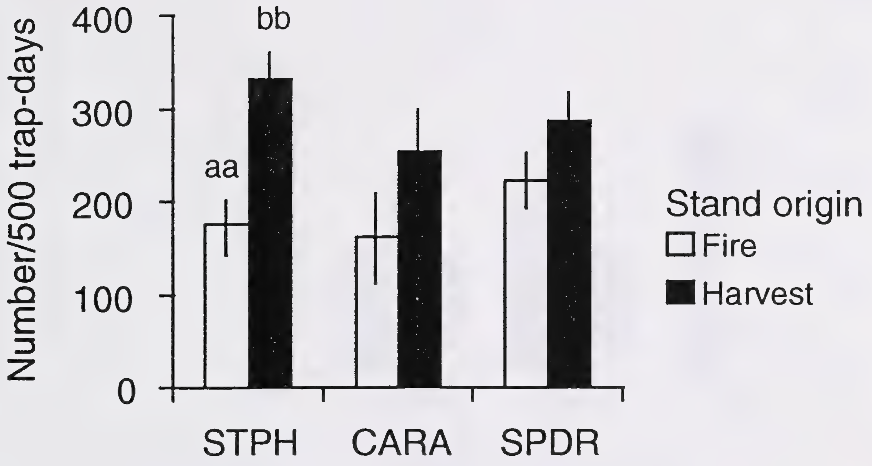


Figure 2. Least Squares Means of Staphylinidae (STPH) and Carabidae (CARA) beetles and spiders (SPDR) by stand origin for year 1 and 2 combined (+/- Standard errors, significant differences indicated at p<.05)

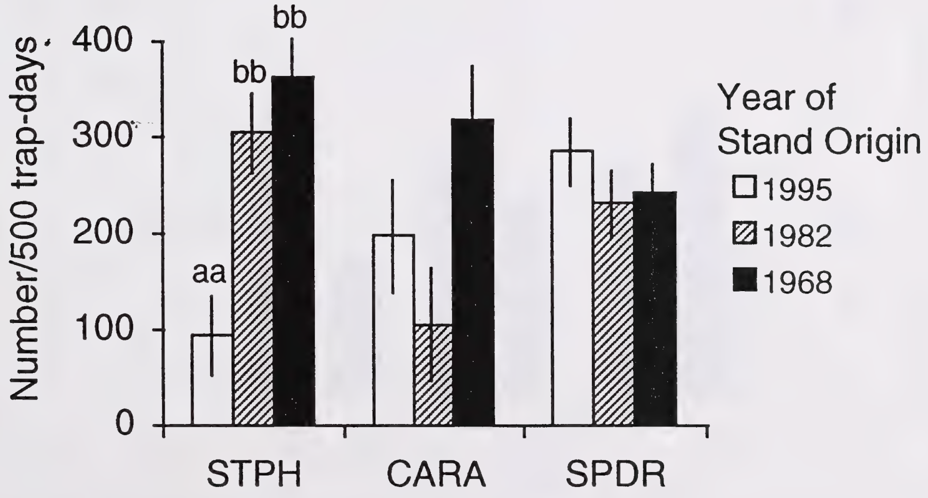


Figure 3. Least Squares Means of Staphylinidae (STPH) and Carabidae (CARA) beetles and spiders (SPDR) by stand age for year 1 and 2 combined (+/- Standard errors, significant differences indicated at p<.05)

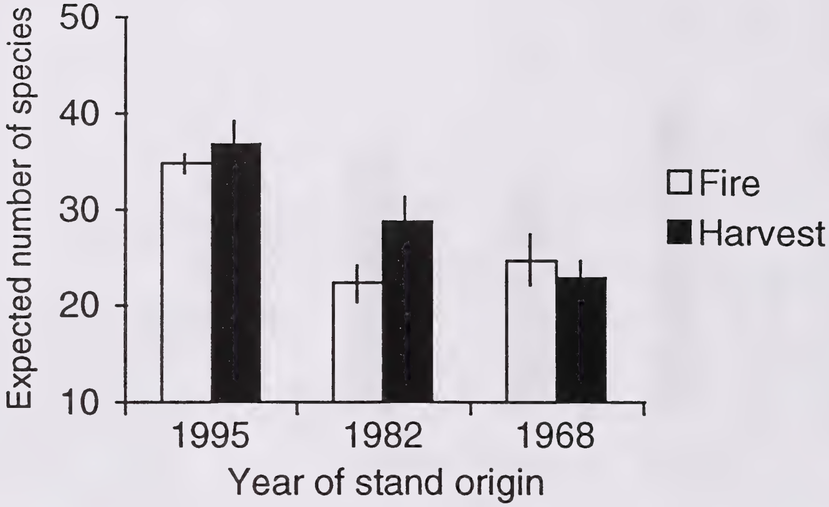


Figure 4*a*. Rarefaction estimates of the expected number of Staphylinidae beetle species (at N=200) from year 1 and year 2 pitfall trap collections by stand age and origin (+/- standard deviation)

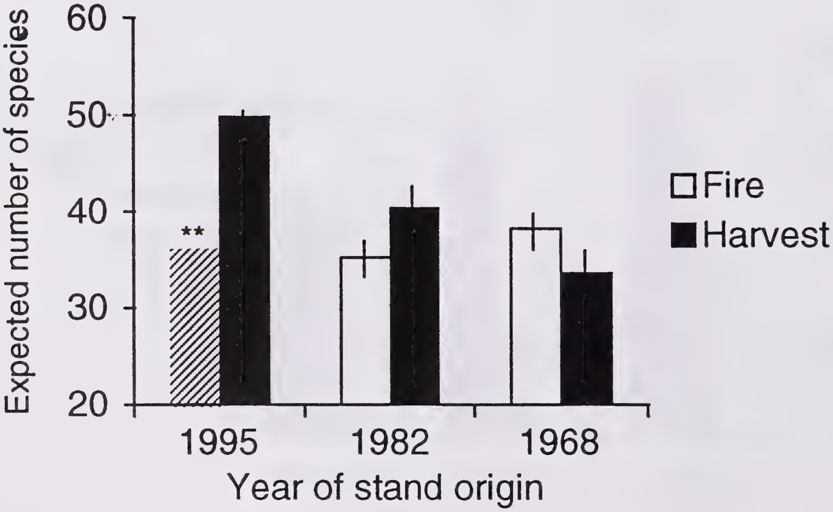


Figure 4*b*. Rarefaction estimates of the expected number of Staphylinidae beetle species (at N=700) from year 1 and year 2 pitfall trap collections by stand age and origin (+/- standard deviation)

**at N=200 (maximum number for Staphylinidae beetles from 1995 Fire stands)

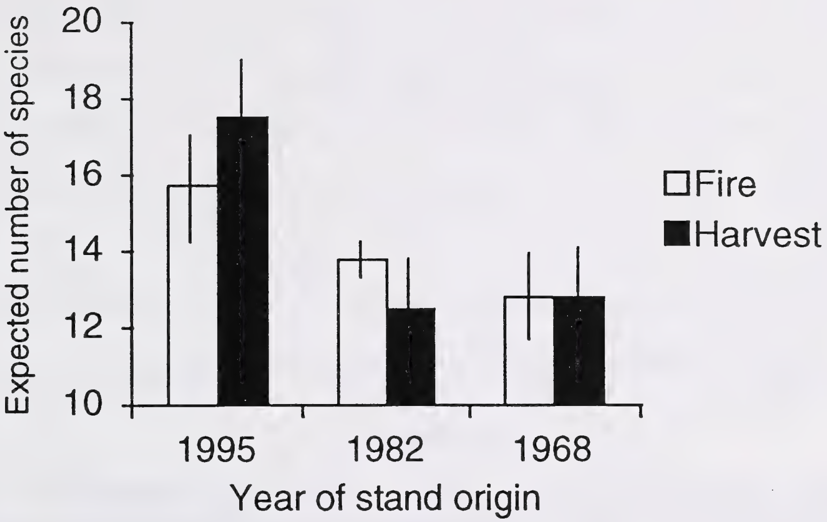


Figure 5. Rarefaction estimates of the expected number of Carabidae beetle species (at N=300) from year 1 and year 2 pitfall trap collections by stand age and origin (+/- standard deviation)

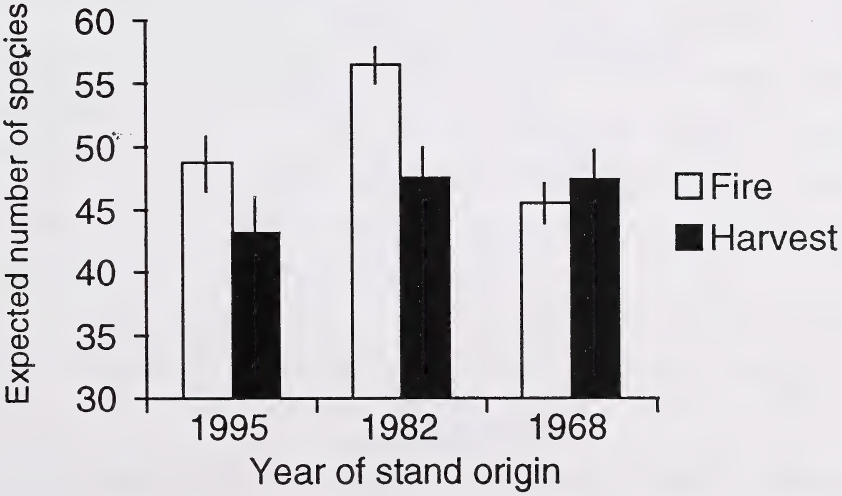


Figure 6. Rarefaction estimates of the expected number of spider species (at N=800) from year 1 and year 2 pitfall trap collections by stand age and origin (+/- standard deviation)

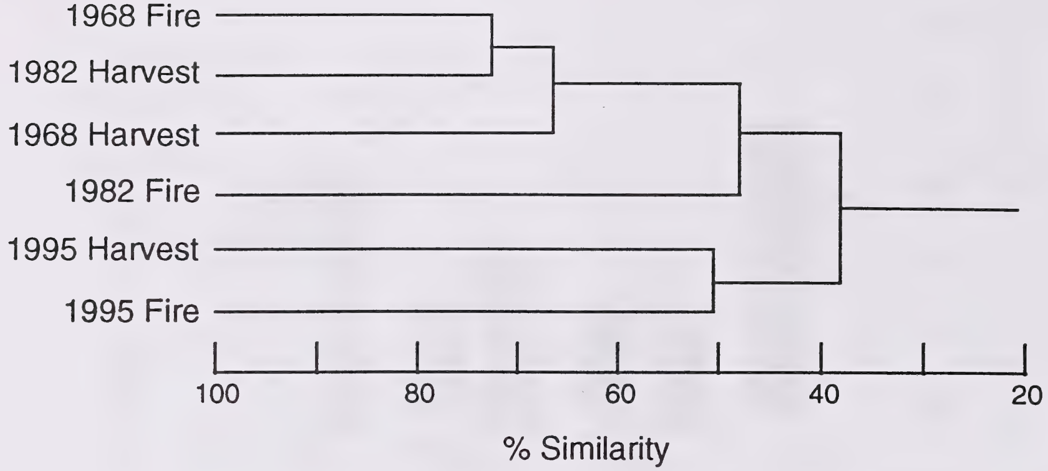


Figure 7. Cluster analysis of Bray-Curtis measures of percent similarity for beetles (Carabidae and Staphylinidae) and spiders collected by pitfall traps in year 1 and year 2 (standardized to 800 trap-days)

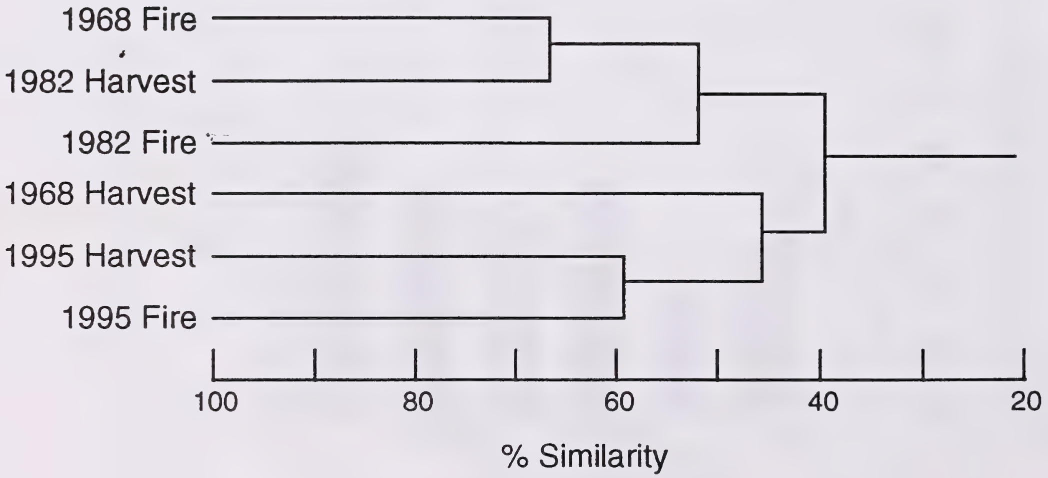


Figure 8*a*. Cluster analysis of Bray-Curtis measures of percent similarity for Carabidae beetles collected by pitfall traps in year 1 and year 2 (standardized to 800 trap-days)

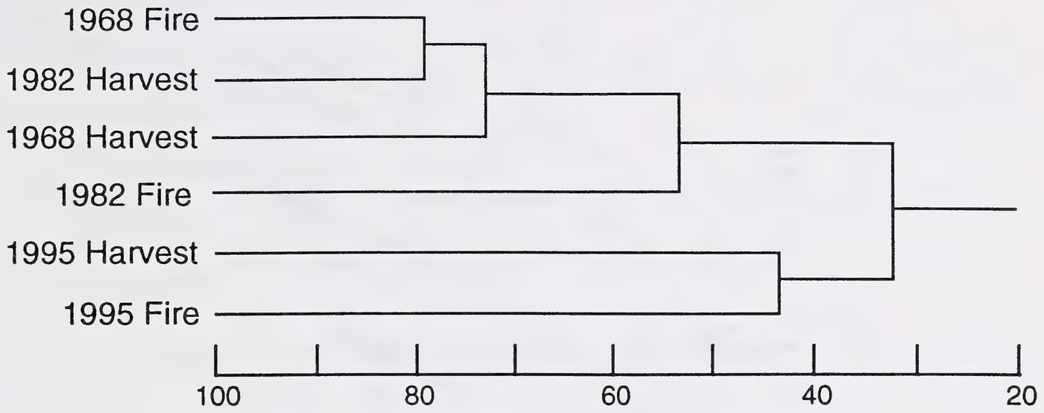


Figure 8*b*. Cluster analysis of Bray-Curtis measures of percent similarity for Staphylinidae beetles collected by pitfall traps in year 1 and year 2 (standardized to 800 trap-days)

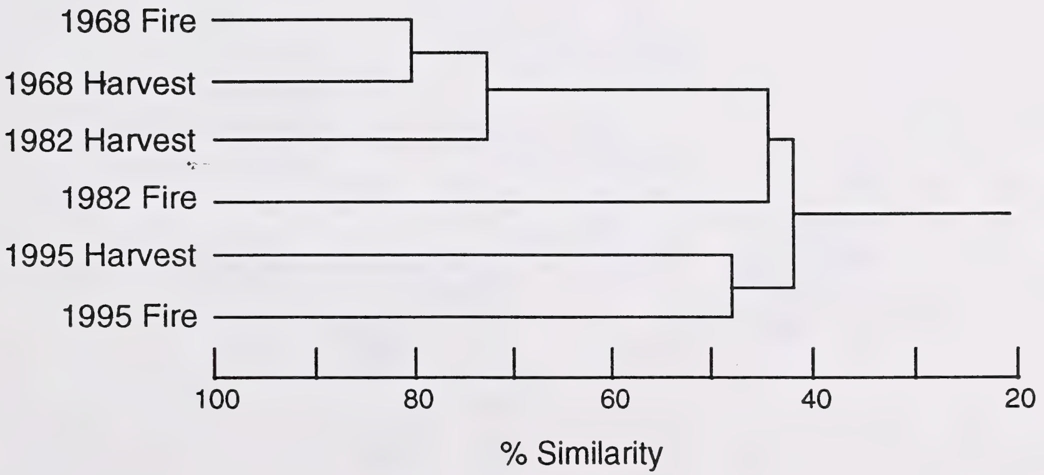


Figure 8*c*. Cluster analysis of Bray-Curtis measures of percent similarity for spiders collected by pitfall traps in year 1 and year 2 (standardized to 800 trap-days)

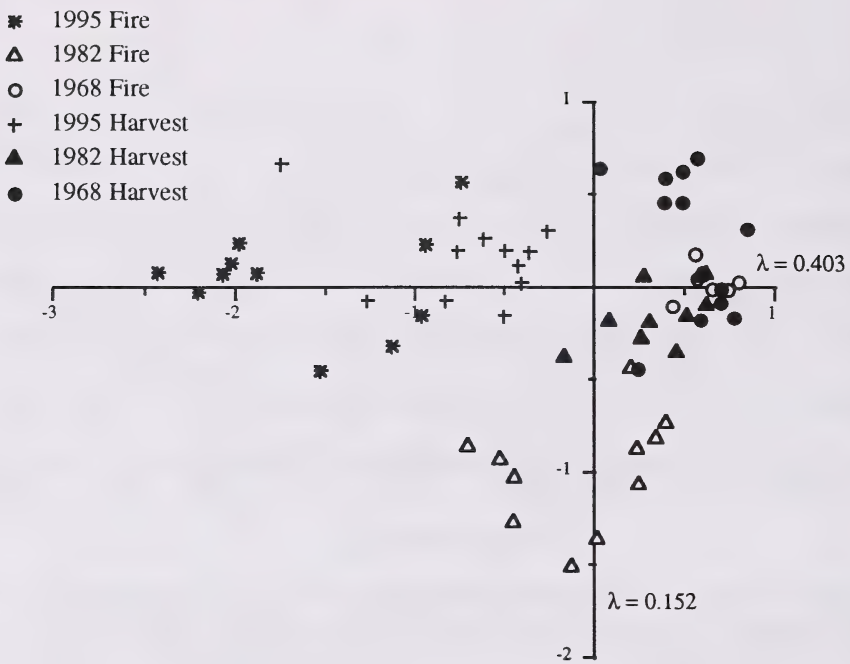


Figure 9. Sample scores from DCA ordination (axis 1 and 2) from 218 species of Carabidae and Staphylindae beetles and spiders (Araneae) collected in year 1 and year 2

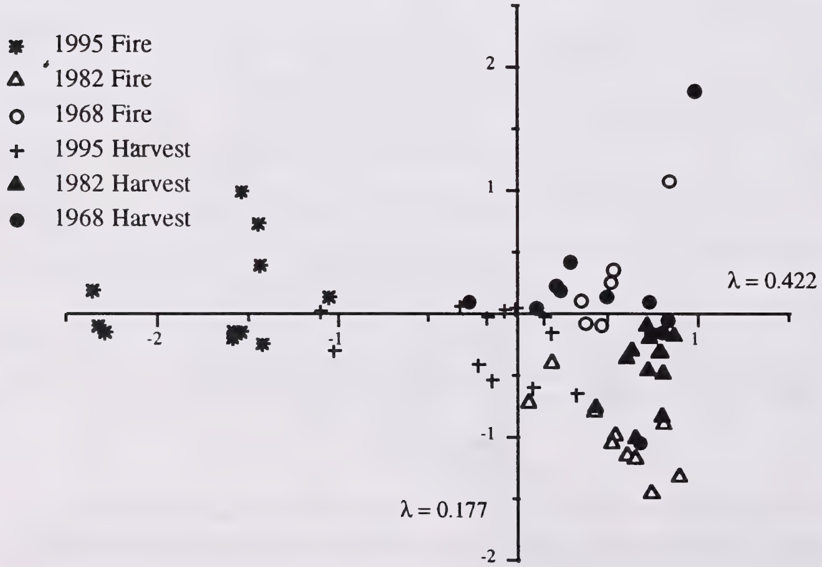


Figure 10*a*. Sample scores from DCA ordination (axis 1 and 2) from 38 species of Carabidae beetles collected in year 1 and year 2

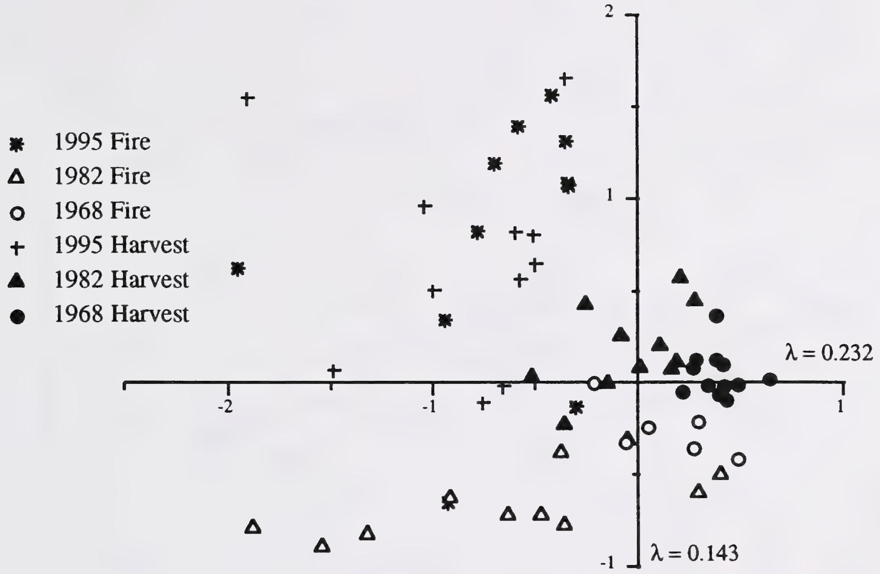


Figure 10*b*. Sample scores from DCA ordination (axis 1 and 2) from 76 species of Staphylinidae beetles collected in year 1 and year 2

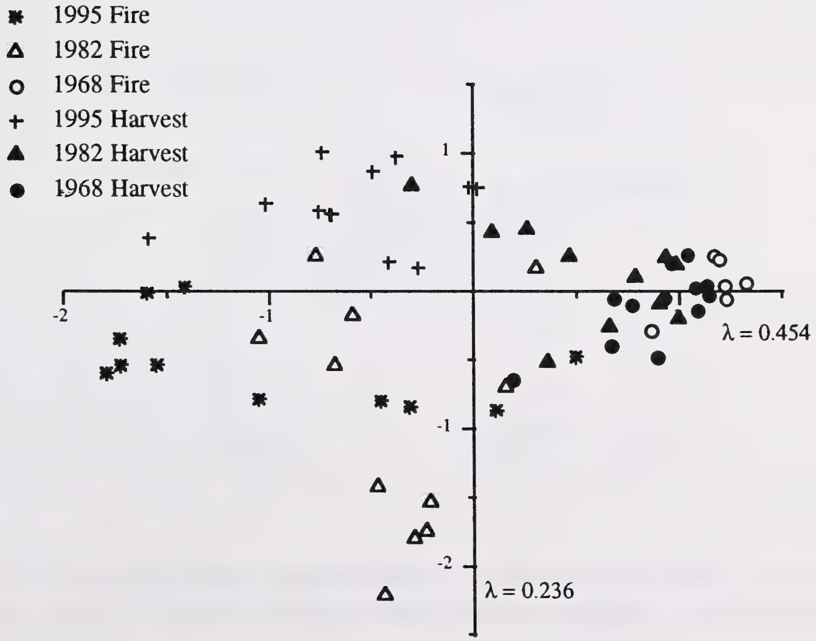
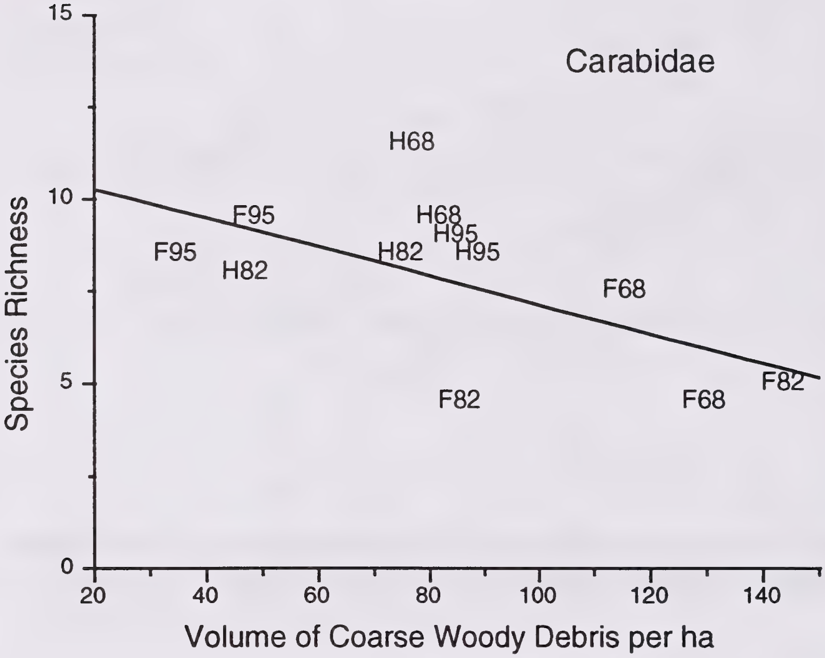


Figure 10*c*. Sample scores from DCA ordination (axis 1 and 2) from 104 species of Spiders (Araneae) collected in year 1 and 2

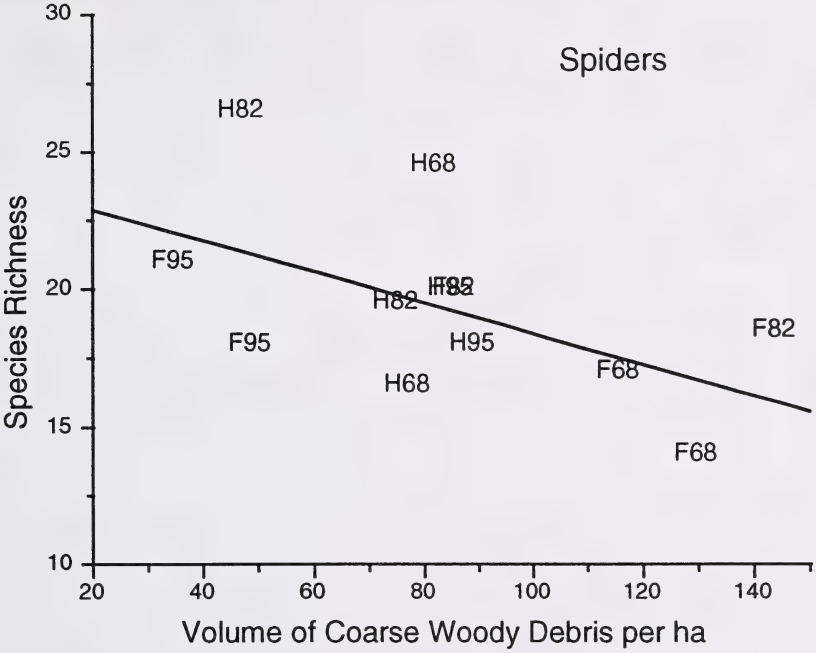


```
Linear Regression::
Y = A + B * X

Parameter Value       Error
------------------------------------------------------------
A         11.04975    1.45406
B         -0.0394     0.01681
------------------------------------------------------------

R         SD          N          P
------------------------------------------------------------
-0.5955   1.83303     12         0.04105
------------------------------------------------------------
```

Figure 11*a*. Linear regression of Carabidae species richness on median volume of Coarse Woody Debris by stand type

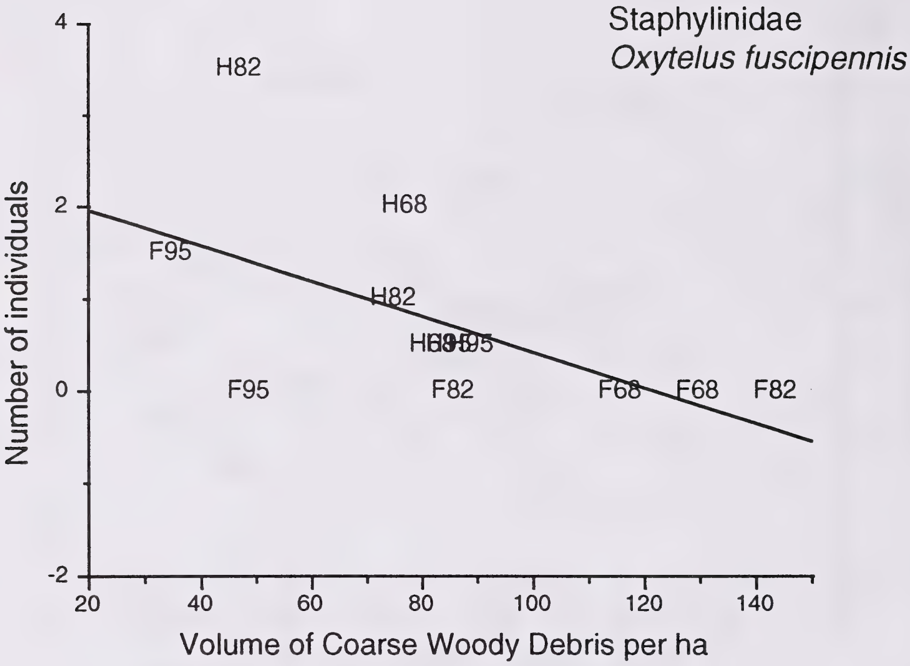


```
Linear Regression:
Y = A + B * X

Parameter Value       Error
------------------------------------------------------------
A         23.98179  2.38304
B         -0.05613  0.02754
------------------------------------------------------------

R         SD         N          P
------------------------------------------------------------
-0.5417   3.00413    12         0.06889
------------------------------------------------------------
```

Figure 11*b*. Linear regression of spider species richness on median volume of Coarse Woody Debris by stand type


Staphylinidae
Oxytelus fuscipennis

```
Linear Regression:
Y = A + B * X

Parameter Value        Error
------------------------------------------------------------
A         2.34672      0.72267
B         -0.0193      0.00835
------------------------------------------------------------

R         SD           N          P
------------------------------------------------------------
-0.5899   0.91102      12         0.04349
------------------------------------------------------------
```

Figure 12. Linear regression of the Staphylinidae beetle, *Oxytelus fuscipennis*, on the median volume of Coarse Woody Debris by stand type

APPENDIX: Species Lists

I. Carabidae species collected by pitfall trap (year 1 and 2 combined)

	Fire			Harvest			Species	
Species	1995	1982	1968	1995	1982	1968	Totals	
Agonum cupreum Dejean	1	0	0	5	0	0	6	
Agonum placidum	2	0	0	1	2	1	6	
Agonum retractum LeConte	9	33	23	78	61	87	291	
Agonum sordens Kirby	153	0	0	13	1	1	168	
Agonum thoreyi	0	0	1	2	1	2	6	
Amara errata	1	0	0	0	0	0	1	*
Amara familiaris	1	0	0	0	0	0	1	*
Amara lunicollis	0	0	0	3	0	0	3	*
Badister obtusus LeConte	0	0	0	1	0	0	1	*
Bembidion nigripes Kirby	0	0	0	1	0	0	1	*
Calasoma frigidum Kirby	4	5	3	7	18	67	104	
Calathus advena LeConte	0	0	0	2	1	2	5	
Calathus ingratus Dejean	37	151	135	70	167	259	819	
Carabus chamissonis Fischer von Waldheim	0	12	0	0	0	1	13	
Cymindis cribricollis Dejean	0	0	0	2	1	1	4	
Elaphrus clairvillei	2	0	0	1	0	0	3	
Elaphrus lapponicus	5	2	0	0	0	0	7	
Harpalus egregius	25	0	0	0	0	0	25	*
Harpalus fulvilabris Mannerheim	0	1	2	0	3	0	6	
Harpalus laticeps LeConte	9	0	0	0	0	0	9	*
Harpalus somnulentus Dejean	0	0	0	0	0	1	1	*
Loricera pilicornis Fabricius	76	0	1	2	0	2	81	
Miscodera arctica Paykull	1	1	0	0	0	0	2	
Nebria gyllenhali castanipes Kirby	0	0	0	0	0	83	83	*
Patrobus foveocollis Eschscholtz	0	22	40	10	23	50	145	
Platynus decentis Say	74	25	231	122	136	479	1067	
Playtnus mannerheimi	0	0	26	0	0	0	26	*
Pterostichus adstrictus Eschscholtz	550	35	118	388	27	517	1635	
Pterostichus haematopus	1	8	0	0	0	2	11	
Pterostichus pensylvanicus LeConte	36	18	28	41	93	82	298	
Pterostichus punctatissimus Randall	12	8	0	0	1	0	21	
Pterostichus riparius Dejean	0	0	4	0	18	205	227	
Scaphinotus marginatus Fischer von Waldheim	4	0	133	66	169	693	1065	
Stereocerus haematopus Dejean	12	1	0	1	0	0	14	
Synuchus impunctatus	0	0	0	2	0	1	3	
Trechus apicalis Motchulsky	0	0	6	7	0	7	20	
Trechus obtusus	0	0	3	4	0	8	15	
Trichocellus cognatus	0	0	0	1	0	0	1	*
Totals	1015	322	754	830	722	2551	6194	

* unique to one stand type

II. Staphylinidae species collected by pitfall trap (year 1 and 2 combined)

			Fire			Harvest		Species	
Species		1995	1982	1968	1995	1982	1968	Totals	
Acidota	crenata (Fabricius)		13	15	8	12	3	51	
Acrolocha	diffusa (Fauvel)			4	12	73	17	106	
Bisnius	siegwaldi (Mannerheim)		1			1		2	
Bolitobius	horni Campbell (in press)		5	2	5	14	5	31	
Bolitobius	sp. 2				2	2		4	
Carphacis	nepigonensis (Bernhauer)				1			1	*
Erichsonius	nanus (Horn)					1		1	*
Eucnecosum	brunnescens (J. Sahlberg)		33	3	26	25	11	125	
Eucnecosum	tenue (LeConte)				3			3	
Eusphalerum	pothos (Mannerheim)	12	1	1	2	11	3	30	
Gabrius	brevipennis (Horn)	1	3	6	1	15	5	40	
Gabrius	microphthalamus (Horn)	1			5			6	
Gabrius	picipennis (Mäklin)	1		1	4	1	1	8	
Habrocerus	schwarzi Horn		35	2	21	25	8	91	
Ischnosoma	fimbriatum Campbell		3	1	4	5	2	15	
Ischnosoma	splendidum (Gravenhorst)	1	8	5	14	8	1	37	
Lathrobium	washingtoni Casey	5	1	3	11	7	3	30	
Lathrobium	fauveli Duvivier	1		2	1	5		9	
Lordithon	bimaculatus (Couper)				1			1	*
Lordithon	fungicola Campbell	17	87	36	29	48	21	238	
Lordithon	thor. thoracicus (Fabricius)	1	2			1	1	5	
Megarthrus	angulicollis Mäklin					1		1	*
Megarthrus	excisus LeConte		1			6		7	
Micropeplus	laticollis Mäklin					1		1	*
Mycetoporus	americanus Erichson		4		9	2	1	25	
Mycetoporus	nigrans Maklin		2					2	
Nitidotachinus	tachyporoides (Horn)			13	2	4	1	20	
Olophrum	boreale (Paykull)				2			2	
Olophrum	consimile (Gyllenhal)	4	1		5			10	
Olophrum	rotundicolle (C.R. Sahlberg)			1	5	1		7	
Omalium	sp. 1	1					1	2	
Omalium	sp. 2				1			1	*
Ontholestes	cingulatus (Gravenhorst)	3	2			7		12	
Oxyporus	occipitalis Fauvel		2	1		1		4	
Oxytelus	fuscipennis Mannerheim	13	3	2	19	39	34	110	
Paederus	littorarius Gravenhorst		1					1	*
Philonthus	concinnus (Gravenhorst)				1			1	*
Philonthus	cruentatus (Gmelin)				1			1	*
Philonthus	cyanipennis (Fabricius)		4	6	4	16	17	47	
Philonthus	politus (Linné)	1						1	*
Philonthus	spiniformis Hatch	1			3	1	1	6	
Philonthus	fulcinius Smetana	2		1		15	11	29	
Philonthus	furvus Nordmann	1			12		1	14	
Proteinus	limbatus Mäklin		2	3		1	1	7	
Pseudopsis	sagitta Herman	2	4	3	12	48	22	91	
Pycnoglypta	aptera Campbell			1				1	*
Quedius	brunnipennis Mannerheim		2	3				5	
Quedius	caseyi caseyi Scheerpeltz		1	8	3	5	7	33	
Quedius	criddlei (Casey)						3	3	
Quedius	frigidus Smetana	1	2					3	
Quedius	fulvicollis (Stephens)	1	1	17	7	22	33	81	
Quedius	lab. labradorensis Smetana	13	31	31	54	53	8	262	
Quedius	mol. molochinoides Smetana			4		1	1	6	
Quedius	nevadensis (Casey)				1			1	*
Quedius	rusticus Smetana	13	3	15	9	49	7	267	
Quedius	simulator Smetana	1	5	3	25	3	7	71	
Quedius	velox Smetana	3	2	38	1	7	41	101	

II. Staphylinidae species collected by pitfall trap (year 1 and 2 combined)

			Fire			Harvest		Species	
Species		1995	1982	1968	1995	1982	1968	Totals	
Staphylinus	capitatus Bland	2		3	11	2	24	42	
Staphylinus	pleuralis LeConte	3	9	37	57	125	91	349	
Stenus	austini Casey		2	3	3	8	9	25	
Stenus	mammops Casey		1	1			1	3	
Tachinus	basalis Erichson	1	29	9		17	21	77	
Tachinus	elongatus Gyllenhal		16	14	22	12	28	92	
Tachinus	frigidus Erichson	9	282	328	3	3	454	1403	
Tachinus	fumipennis (Say)	3	67	294	37	52	152	1982	
Tachinus	quebecensis Robert	3	89	39		42	134	307	
Tachinus	thruppi Hatch	2		2			7	11	
Tachinus	vergatus Campbell			1				1	*
Tachyporus	abdominalis (Fabricius)						2	2	
Tachyporus	borealis Campbell	1			2	3	2	8	
Tachyporus	flavipennis Campbell	1						1	*
Tachyporus	maculicollis LeConte	3		1	4	1		9	
Tachyporus	mexicanus Sharp	1			2			3	
Tachyporus	nitidulus (Fabricius)				1			1	*
ALEOCHARINAE	(Uknown)	3	461	211	125	286	336	1449	
Unknown			4	2	2	7	8	23	
	Totals:	213	1261	1203	721	1869	2591	7858	

* unique to one stand type

III. Spider species collected by pitfall trap (year 1 and 2 combined)

		Fire			Harvest		Species	
Species	1995	1982	1968	1995	1982	1968	Totals	
Agelenopsis utahana (Chamb. and Ivie)	6	8	2	1	9	10	36	
Agroeca ornata Banks	7	42	91	25	63	78	306	
Agyneta olivacea (Em.)	0	2	1	1	2	3	9	
Allomengea dentisetis (Grube)	41	64	105	235	184	201	830	
Alopecosa aculeata (Clerck)	43	68	17	13	1	1	143	
Amaurobius borealis Em.	5	9	84	23	173	102	396	
Arctobius agelenoides (Em.)	0	0	0	0	0	0	0	
Arctosa alpigena (Doleschall)	15	0	0	1	0	0	16	
Arctosa emertoni Gertsch	1	0	2	0	0	0	3	
Arctosa raptor (Kulczynski)	0	1	0	0	0	1	2	
Bathyphantes pallidus (Banks)	9	16	67	29	144	82	347	
Bianor aemulus (Gertsch)	0	0	4	0	1	1	6	
Ceraticelus fissiceps (O.P.-Cambridge)	0	2	0	1	5	1	9	
Ceraticelus laetabilis (O.P.-Cambridge)	1	1	0	2	0	0	4	
Ceratinella alaskae Ch. & I.	0	0	1	0	0	0	1	*
Ceratinella brunnea Em.	1	1	0	0	0	0	2	
Ceratinopsis stativa (Simon)	1	1	0	0	2	0	4	
Clubiona canadensis Em.	1	2	3	0	0	7	13	
Clubiona furcata Em.	1	0	0	0	0	0	1	*
Clubiona kulczynskii Lessert	2	5	2	4	10	10	33	
Clubiona moesta Banks	0	1	0	0	0	0	1	*
Clubiona opeongo Edwards	0	0	0	0	2	0	2	*
Clubiona sp. A	0	0	0	0	0	1	1	*
Cnephalocotes obscurus (Blackwall)	0	0	0	1	0	0	1	*
Collinsia clypiella (Chamb.)	0	0	0	0	1	0	1	*
Cryphoeca exlinae Roth	0	0	1	0	0	1	2	
Cybaeopsis euopla (Bishop and Crosby)	70	19	184	87	125	174	659	
Diplocentria bidentata (Em.)	9	8	10	11	32	10	80	
Diplocephalus subrostratus (O.P.-Cambridge)	1	1	0	1	0	1	4	
Drassodes neglectus (Keys.)	0	0	0	1	0	0	1	*
Drassyllus niger (Banks)	0	0	0	0	0	1	1	*
Eperigone trilobata (Em.)	1	0	0	5	1	0	7	
Ero canionis Chamb. & Ivie	0	0	0	0	1	0	1	*
Euryopis argentia Em.	0	0	2	0	1	0	3	
Evarcha hoyi (P&P)	0	0	0	1	0	0	1	*
Gnaphosa borea Kulczynski	11	14	4	0	0	0	29	
Gnaphosa brumalis Thorell	3	3	0	1	1	0	8	
Gnaphosa microps Holm	12	26	1	4	5	0	48	
Gnaphosa muscorum(L.Koch)	5	6	0	0	1	1	13	
Gnaphosa parvula Banks	3	8	0	14	1	1	27	
Gonatium crassipalpum Bryant	0	0	0	1	1	2	4	
Grammonata gigas (Banks)	0	1	0	0	3	0	4	
Hahnia arizonica Chamberlin	0	0	0	0	1	0	1	*
Haplodrassus hiemalis (Em.)	5	16	2	6	4	5	38	
Haplodrassus signifer (C.L. Koch)	1	1	0	0	0	0	2	
Helophora insignis (Blackwall)	10	9	6	4	9	15	53	
Hybauchenidium gibbosum (Sorenson)	4	8	8	0	32	7	59	
Hyposinga rubens (Hentz)	1	2	0	0	0	0	3	
Hypselistes florens (O.P.-Cambridge)	0	1	0	1	2	0	4	
Larinicides patagiatus (Clerck)	0	1	0	0	0	0	1	*
Lepthyphantes alpinus (Em.)	1	0	1	1	1	1	5	
Lepthyphantes complicatus (Em.)	0	1	5	0	3	1	10	
Lepthyphantes intricatus Em.	1	2	100	61	135	144	443	
Micaria aenea Thorell	0	3	0	2	0	2	7	
Micaria pulicaria (Sundervall)	0	0	1	2	1	4	8	
Micaria tripunctata Holm	0	1	0	0	0	0	1	*
Microneta viaria (Blackwall)	0	3	6	1	4	13	27	

III. Spider species collected by pitfall trap (year 1 and 2 combined)

Species	Fire 1995	 1982	 1968	Harvest 1995	 1982	 1968	Species Totals	
Neriene clathrata (Sund.)	0	0	0	0	2	1	3	
Oedothorax trilobatus (Banks)	0	0	1	0	0	0	1	*
Oreonetides rectangulatus (Em.)	0	0	0	1	0	0	1	*
Oreonetides recurvatus (Em.)	0	0	3	1	3	4	11	
Oreonetides sp. A	1	0	1	1	0	1	4	
Oreonetides vaginatus (Thorell)	8	7	10	5	6	6	42	
Orodrassus canadensis Platnick & Shadab	0	1	0	0	0	0	1	*
Ozyptila sincera canadensis Dondale and Redne	0	2	21	16	7	3	49	
Pardosa (unplaced female)	0	0	0	2	0	0	2	*
Pardosa furcifer(Thorell)	0	0	0	1	0	0	1	*
Pardosa fuscula (Thorell)	9	4	1	81	9	1	105	
Pardosa hyperborea (Thorell)	36	2	0	20	2	1	61	
Pardosa mackenziana (Keys.)	136	193	67	129	106	116	747	
Pardosa moesta Banks	119	101	17	644	242	31	1154	
Pardosa tesquorum (Odenwall)	0	0	0	4	0	0	4	*
Pardosa uintana Gertsch	94	13	0	1	0	0	108	
Pardosa xerampelina (Keys.)	282	76	9	234	30	8	639	
Pirata bryantae Kurata	13	1	0	2	1	0	17	
Pityohyphantes costatus (Hentz)	1	1	0	0	0	0	2	
Pocadicnemis americana Millidge	0	0	0	0	0	1	1	*
Robertus fuscus (Em.)	1	1	2	0	1	1	6	
Sciastes truncatus (Em.)	2	4	3	0	9	2	20	
Scironis tarsalis Em.	0	0	0	0	0	2	2	*
Sisicottus montanus (Em.)	3	0	1	1	1	1	7	
Sisicottus nesides (Chamb.)	0	0	0	0	0	1	1	*
Thanatus formicinus (Clerck).	1	0	0	0	0	0	1	*
Thanatus striatus C.L. Koch	0	0	0	3	0	0	3	*
Theridion sexpunctatum Em.	0	0	0	0	1	1	2	
Tibellus oblongus (Walckenaer)	0	1	0	0	0	0	1	*
Trochosa terricola Thorell	21	61	29	5	52	55	223	
Tunagyna debilis (Banks)	1	0	0	1	14	0	16	
Walckenaeria atrotibialis O.P.-C	0	0	1	0	0	0	1	*
Walckenaeria castanea (Em.)	8	3	15	2	12	17	57	
Walckenaeria directa (O.P.-Cambridge)	0	10	8	2	7	14	41	
Walckenaeria exigua Millidge	0	1	0	0	0	0	1	*
Walckenaeria karpinskii (O.P.-Cambridge)	0	0	1	0	0	0	1	*
Xysticus britcheri Gertsch	0	0	0	1	0	0	1	*
Xysticus canadensis Gertsch	0	0	0	0	0	1	1	*
Xysticus durus (Soerensen)	2	0	0	0	0	0	2	*
Xysticus elegans Keys.	0	0	1	0	4	1	6	
Xysticus ellipticus Turnbull et al.	0	0	0	1	0	0	1	*
Xysticus emertoni Keys.	17	1	4	28	4	21	75	
Xysticus ferox (Hentz)	0	0	0	1	0	0	1	*
Xysticus luctuosus (Blackwall)	8	10	17	8	22	38	103	
Zelotes fratris Chamberlin	1	13	2	7	12	6	41	
Zornella cultrigera (L.Koch)	4	2	43	12	15	53	129	
Erigoninae sp. A	0	0	0	1	0	0	1	*
Erigoninae sp. B (unpaced female)	0	0	0	0	0	1	1	*
Erigoninae sp. C (unplaced female)	0	0	0	0	1	0	1	*
Erigoninae sp. D	1	0	0	0	0	0	1	*
totals	1041	865	967	1755	1524	1269	7421	

* unique to one stand type

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